

AGE AND GROWTH OF RED SNAPPER,
Lutjanus campechanus, LUTJANIDAE,
COLLECTED ALONG THE SOUTHEASTERN
UNITED STATES FROM NORTH CAROLINA
THROUGH THE EAST COAST OF FLORIDA

CHARLES S. MANOOCH, III and JENNIFER C. POTTS

National Marine Fisheries Service
Southeast Fisheries Science Center
Beaufort Laboratory
Beaufort, NC 28516-9722

Abstract: Opaque bands on sectioned sagittal otoliths ($n = 537$) were used to age red snapper, *Lutjanus campechanus*, sampled from recreational headboat and commercial hook and line landings, and fishery-independent hook and line and trap samples from Beaufort, North Carolina through the Florida Keys, 1990–1996. Rings could be counted on 97.4% of the otolith sections, and 87.5% were legible enough to record growth measurements. Marginal increment analysis revealed that annuli form March through May. The maximum estimated age and total length for the species was age 25 yr and 955 mm. Mean back-calculated total lengths at ages 1, 5, 10, 15, 20, and 25 years were 172-, 491-, 702-, 792-, 860-, and 922-mm, respectively. The von Bertalanffy growth equation was $L_t = 955 (1 - e^{-0.146(t-0.182)})$, where t = age in years. The length-weight relationship for red snapper was $W = 1.5 \times 10^{-8} L^{2.99}$, where W = whole weight in kilograms. The following linear relationships in millimeters were calculated to convert fish lengths: $TL = -3.21 + 1.08 (FL)$; $TL = 10.26 + 1.24 (SL)$; and $FL = 11.67 + 1.15 (SL)$. A fish age-fish length key was also developed.

Key Words: red snapper, age and growth, southeastern U.S., Lutjanidae.

INTRODUCTION

The red snapper, *Lutjanus campechanus* (Lutjanidae), is considered to be the most prized species of the snapper-grouper complex along the southeastern coast of the United States. It consistently ranks above the Florida pompano, *Trachinotus carolinus*, as the most valuable commercial species of finfish on a price per pound basis. From 1990 through 1996, red snapper retailed at dockside for \$2.00 to \$3.00 per pound. Despite the species' value to fishermen on a price per pound basis, with the exception of Georgia, its total poundage value rarely ranks among the top 10 market finfish in commercial fisheries of the southeastern United States.

Red snapper are distributed throughout the Gulf of Mexico and along the Atlantic coast to North Carolina, occasionally to Massachusetts. It occurs in the western Atlantic throughout the Exclusive Economic Zone (EEZ) and territorial seas, and is an important component of the catch in the deeper shelf waters (deeper than 20 m) (SAFMC, 1983). Off the southeastern United States, the red snapper typically occurs in depths of 50 to 100 m over low- and high-relief hard bottom (Manooch, 1984).

Table 1. Observed mean total length (TL) at age for red snapper off the southeastern U.S.

Age	N	Mean TL (mm)	Standard Deviation	Range (mm, TL)
1	4	213	10.9	197–220
2	17	272	30.7	233–338
3	81	366	36.8	245–425
4	121	419	35.7	360–515
5	95	506	37.6	430–598
6	75	587	47.1	492–680
7	63	637	43.4	557–730
8	22	688	57.5	610–780
9	9	750	28.9	710–787
10	6	763	11.7	747–780
11	7	792	17.6	780–827
12	3	813	48.5	757–842
13	4	820	23.1	800–852
14	7	822	21.7	787–850
15	1	840		
16	2	868	31.8	845–890
17	1	865		
20	3	886	26.6	855–902
23	1	900		
25	1	937		
Total	523			

Lutjanus campechanus is an opportunistic bottom feeder that consumes a variety of invertebrates and small fishes. It remains the same sex throughout its lifespan, and maturity may occur as early as the second year of life (SAFMC, 1983). Spawning extends through the warmer months, beginning as early as April off North Carolina; spawning in the Gulf of Mexico usually extends from May through September (SAFMC, 1983). Spawning grounds of the species are not well known, although fishermen off Texas reported ripe females at depths of 37 m, and two spawning areas off Panama City, Florida, were found at water depths between 18–37 m (SAFMC, 1983). Females, as small as 250 mm, and males, as small as 225 mm, have been documented as sexually mature. Free-floating eggs have been hatched in the laboratory in 24–27 hr, and the larvae fed three days after hatching (Manooch, 1984). Red snapper are relatively slow growing, and may attain a length of approximately 950 mm and age-25 (this study).

We conducted an updated examination of age and growth using sectioned sagittal otoliths collected from the headboat and commercial fisheries operating from North Carolina through the Florida Keys. Additional specimens were obtained by fishery-independent sampling. Specifically, we validated rings on otoliths as being annuli, calculated fish length at the time of annulus formation, derived theoretical growth parameters, constructed fish age-length keys, and derived weight-length and length-length relationships.

MATERIALS AND METHODS

Collection and examination of otoliths.—Since an earlier age study by Nelson and Manooch (1982) on red snapper was dated and utilized samples from the 1970's, we decided to update age and growth information on the species with

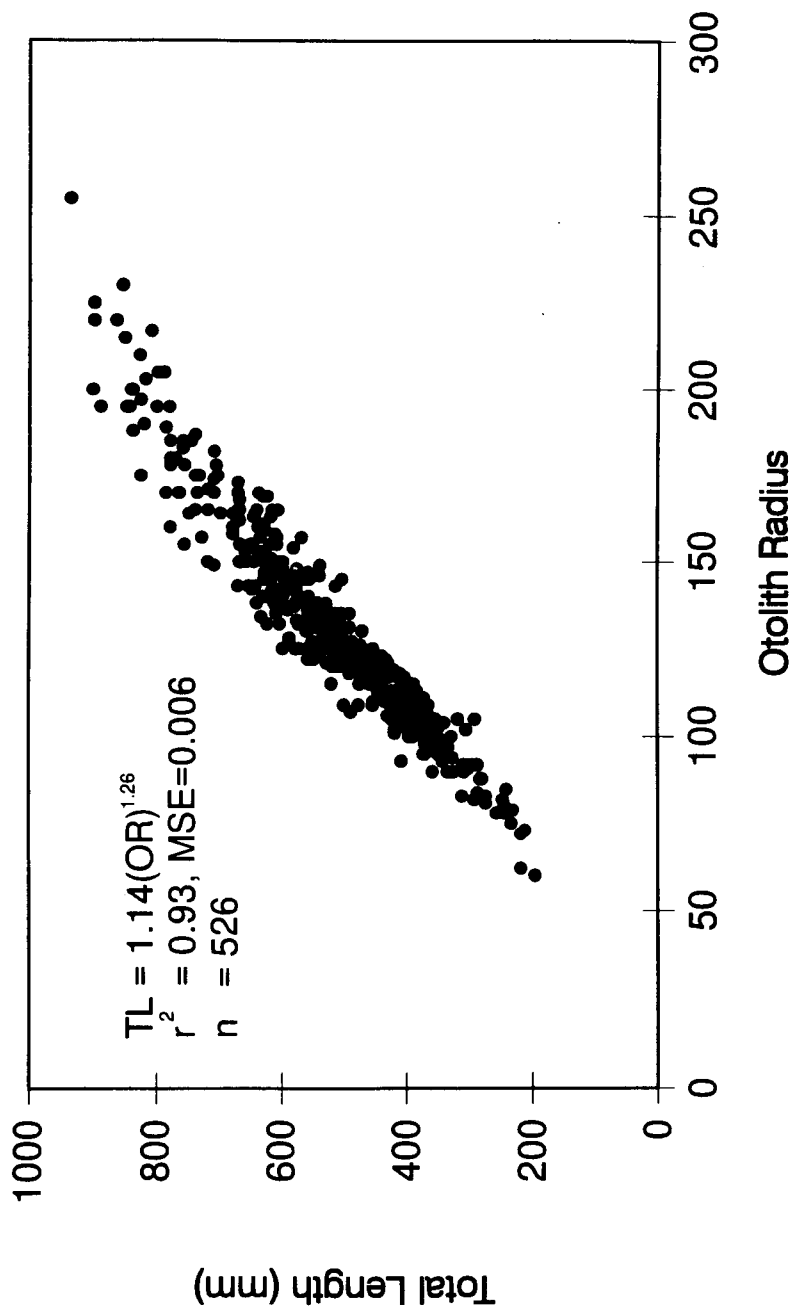


FIG. 1. Otolith radius-total length relationship of red snapper off the southeastern U.S.

Table 2. Mean back-calculated total lengths in mm (± 1 SE) based on the ln-ln proportional equation for red snapper off the southeastern U.S.

Age	N	Age (Rings)									
		1	2	3	4	5	6	7	8	9	10
1	4	176 \pm 7.2									
2	16	166 \pm 3.8	231 \pm 4.7								
3	77	165 \pm 2.0	252 \pm 3.0	331 \pm 3.9							
4	107	167 \pm 1.5	251 \pm 1.9	331 \pm 2.3	388 \pm 2.7						
5	81	177 \pm 1.4	268 \pm 2.2	352 \pm 2.8	422 \pm 3.5	479 \pm 4.1					
6	67	175 \pm 1.7	271 \pm 2.9	361 \pm 3.9	436 \pm 4.6	502 \pm 5.0	559 \pm 5.7				
7	53	174 \pm 2.0	268 \pm 2.8	361 \pm 3.9	436 \pm 4.4	502 \pm 5.1	560 \pm 5.8	611 \pm 6.1			
8	22	177 \pm 2.9	273 \pm 3.6	371 \pm 6.5	443 \pm 7.5	507 \pm 8.6	563 \pm 10.1	616 \pm 11.1	662 \pm 12.0		
9	9	177 \pm 4.3	276 \pm 7.0	370 \pm 8.3	448 \pm 9.1	516 \pm 11.4	581 \pm 12.1	631 \pm 11.5	677 \pm 11.9	721 \pm 11.7	
10	6	178 \pm 5.6	275 \pm 9.6	361 \pm 9.7	436 \pm 14.1	498 \pm 14.6	559 \pm 19.3	611 \pm 21.8	653 \pm 18.2	695 \pm 14.6	733 \pm 8.5
11	6	171 \pm 4.0	262 \pm 4.6	346 \pm 6.3	420 \pm 10.3	485 \pm 9.1	546 \pm 10.8	599 \pm 9.3	652 \pm 6.0	698 \pm 4.6	739 \pm 4.3
12	3	182 \pm 8.7	271 \pm 9.3	354 \pm 6.2	421 \pm 17.9	472 \pm 18.9	522 \pm 18.8	585 \pm 10.6	624 \pm 10.1	672 \pm 9.6	721 \pm 10.8
13	4	156 \pm 4.0	238 \pm 1.1	320 \pm 0.5	386 \pm 7.2	443 \pm 8.0	496 \pm 7.7	543 \pm 8.6	595 \pm 12.1	645 \pm 18.7	691 \pm 18.8
14	7	165 \pm 3.1	253 \pm 3.9	334 \pm 4.9	397 \pm 5.1	451 \pm 3.5	498 \pm 4.9	545 \pm 5.8	587 \pm 6.7	632 \pm 6.8	673 \pm 5.8
15	1	184	269	351	432	469	516	564	613	662	688
16	2	179 \pm 1.5	270 \pm 3.1	340 \pm 5.3	397 \pm 11.4	464 \pm 3.5	534 \pm 0.2	575 \pm 1.1	612 \pm 12.4	652 \pm 16.2	686 \pm 19.8
17	1	165	261	329	390	454	511	555	586	632	678
20	2	177 \pm 13.3	256 \pm 19.6	331 \pm 31.9	387 \pm 38.3	445 \pm 49.6	500 \pm 51.6	548 \pm 55.1	589 \pm 50.8	627 \pm 55.3	662 \pm 47.6
23	1	192	272	353	416	481	548	616	662	700	723
25	1	150	224	288	358	415	474	534	575	595	616
Total N/ Weighted Mean TL	470	172	261	346	417	491	555	603	642	675	702

contemporary samples. This was done so that a subsequent assessment of the population could be completed using the best information available.

Otoliths were collected by various state agency port samplers and the National Marine Fisheries Service (NMFS) from headboats and commercial hook and line fishing vessels from Beaufort, North Carolina, through the Florida Keys (n = 331). Additional otoliths (n = 206) were obtained by the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) Program. These fishery-independent samples were collected by employees of the South Carolina Department of Natural Resources, Charleston, South Carolina. The total number of otoliths examined was 537.

Sagittae were removed from the cranium by opening the *otic bulla* with a wood chisel from under the operculum. Otoliths were stored dry in coin envelopes. Fish weight (kg), total length (TL mm), date, and area of capture were recorded on each envelope. Fork length (FL mm) and standard length (SL mm) were recorded for some fish (n = 206). Using a high-speed technique developed by Cowan et al. (1995), sagittal otoliths were ground down along the transverse plane (dorsoventral), to produce 0.50 mm thin sections. Sections were polished on a 1,200 grit wet/dry sand paper to remove micro-scratches incurred by grinding.

Otolith sections were examined under a dissecting microscope (25 \times) using reflected light and viewed with a camera/video monitor system. Two types of rings were visible in the sections: an opaque ring that appeared white, and a translucent ring that was dark. Lateral measurements from the otolith focus to each opaque ring and to the otolith margin were recorded by hand from the monitor screen, then transferred to a microcomputer for analysis.

Validation.—Marginal increment analysis was used to determine if opaque rings were annual, and could therefore, be called annuli. Monthly mean distance

Table 2. Extended.

11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
771±6.6														
762±15.7	790±20.9													
737±19.4	772±17.9	796±14.8												
711±6.9	750±8.3	780±8.5	804±8.5											
713	739	764	790	816										
711±23.2	743±24.2	762±22.1	787±20.1	812±23.6	839±24.4									
706	729	748	772	795	819	843								
697±40.0	728±36.0	751±36.1	770±33.4	789±30.7	811±25.7	828±25.2	846±24.6	858±23.5	871±22.4					
742	757	771	785	805	819	834	849	858	868	879	888	898		
637	658	679	700	721	743	764	786	807	829	851	823	909	922	
730	752	770	786	792	812	820	832	846	860	865	880	896	909	922

plots of the last ring to the otolith margin for age groups 1–6 combined were analyzed. If the rings were formed once each year, then the plot should reveal a minimum ring-to-margin increment followed by increased increment width as additional growth followed annulus formation. We also identified months where marginal increments equaled zero as the period when the annuli were formed.

Back-calculated growth.—The fish length and otolith radius relationship was described by regressing the log-transformed fish length on log-transformed otolith radius (R_c). The linearized equation was $\ln(L) = a + b \ln(R_c)$, where L = total length in mm. The back-calculated total lengths at each age were determined from the log transformed, otolith proportional equation (Carlander, 1981; Johnson et al., 1994):

$$L_A = \exp[a + (\ln L_c - a) * (\ln R_A / \ln R_c) + \text{MSE}/2],$$

where

L_A = back-calculated length to annulus A,

a = intercept from the log transformed total
length-otolith radius regression,

L_c = total length at capture,

R_A = otolith radius to annulus A,

R_c = total otolith radius at capture, and

MSE = mean square error (σ^2) from regression used
to correct for the transformation bias.

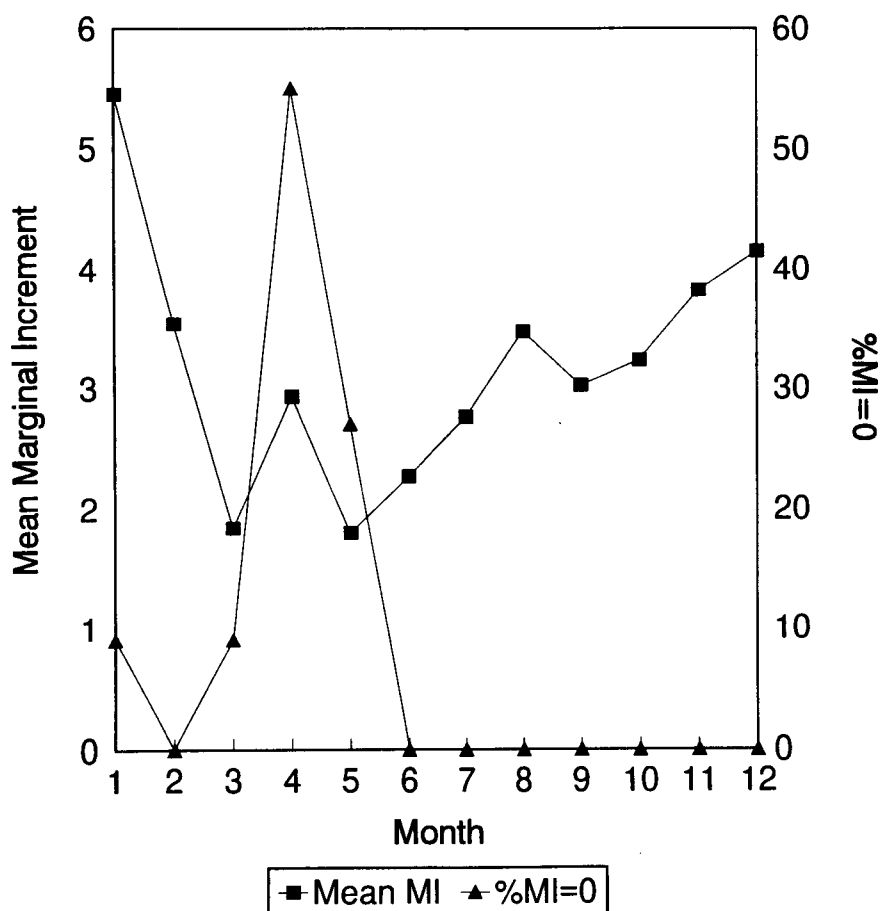


FIG. 2. Marginal increment analysis for red snapper off the southeastern U.S.

Growth parameters.—Growth parameters, L_{∞} (asymptotic fish length), K (growth coefficient), and age at beginning of growth (t_0) were used to construct theoretical growth models. These parameters were derived from the von Bertalanffy equation: $L_t = L_{\infty} (1 - \exp [-K (t - t_0)])$, which is the most widely used growth model in fisheries and is fitted to back-calculated length-at-age data (Ricker, 1975; Everhart et al., 1981). Two equations were derived: one using all the back-calculated data; the other using back-calculated data from the last ring only (Vaughan and Burton, 1994). Growth parameters were estimated using SAS PROC NLIN with the Marquardt Option (SAS Institute, 1982), and we weighted the data by the number of fish sampled at each age.

Size relationships.—To describe the relationship of fish weight to fish length we used log-log regression and transformed the equation to: $\ln W = a + b \ln TL$, where W = weight in kilograms, and TL = total length in millimeters. Linear relationships: $TL = a + b (FL)$, $TL = a + b (SL)$, and $FL = a + b (SL)$ were used to convert lengths, where TL = total length, FL = fork length, and SL = standard length, were in millimeters.

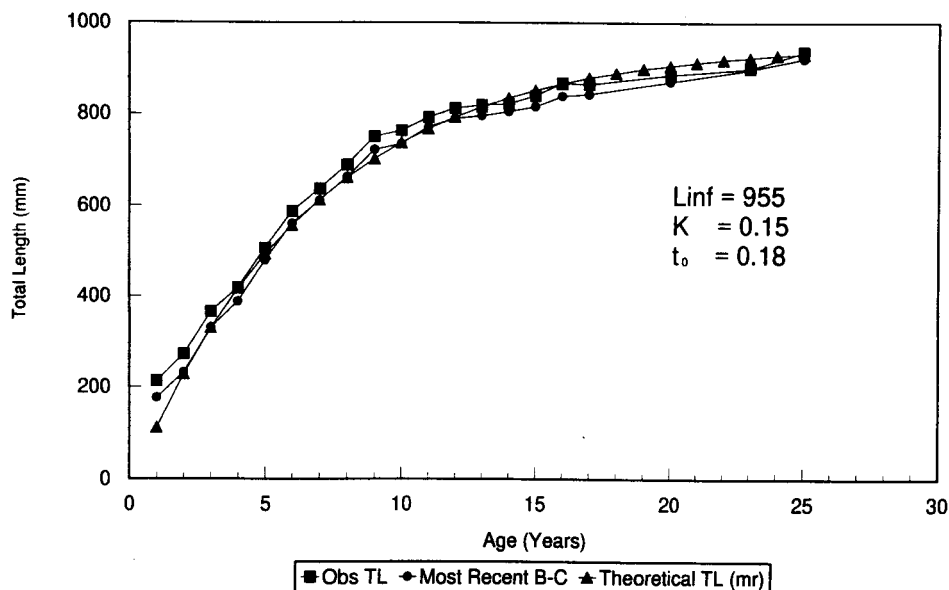


FIG. 3. Mean observed, back-calculated (last annulus data, ln-ln proportional equation), and theoretical (mr = most recent) total lengths for red snapper off the southeastern U.S.

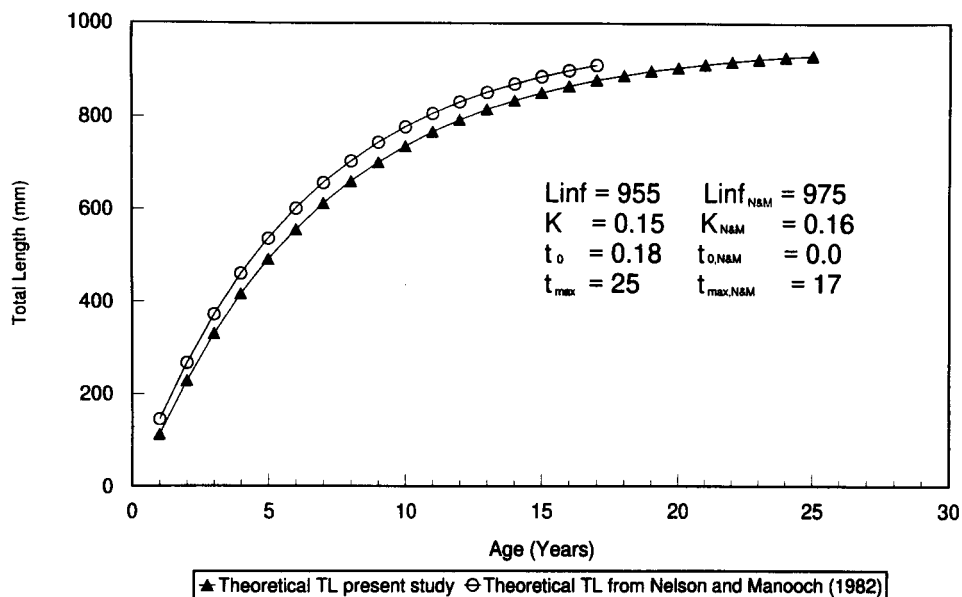


FIG. 4. Comparison of theoretical growth equations from present study and Nelson and Manooch (1982) ($L_{\infty} = L$ infinity).

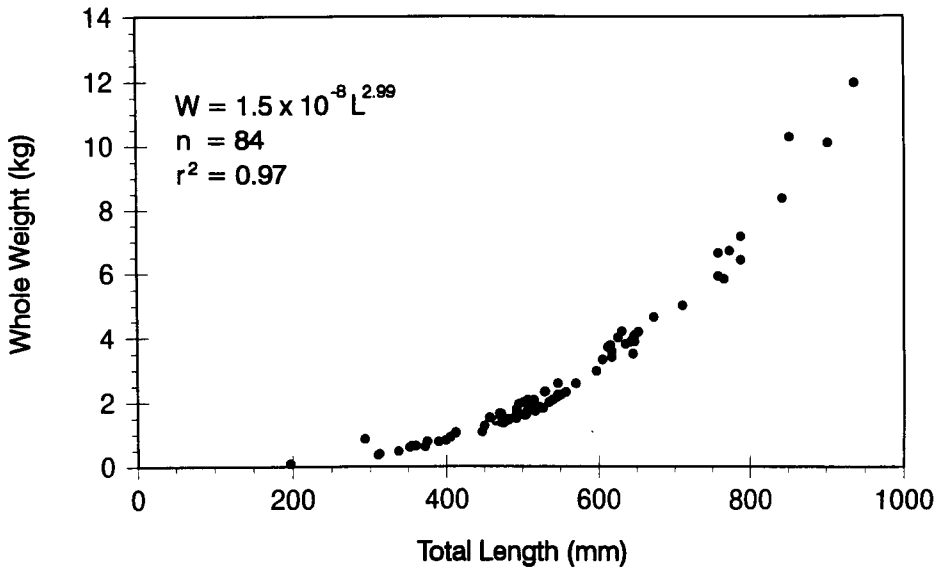


FIG. 5. Total length (mm)-whole weight (kg) relationship for red snapper off the southeastern U.S.

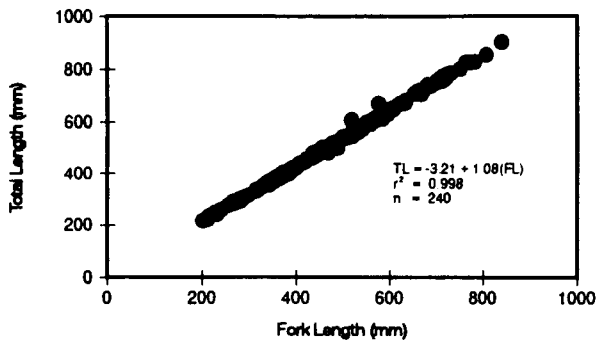
Fish age-fish length key.—Observed ages at lengths (lengths of red snapper at the time of capture for each age) were used to obtain an age-length key. Fish for which we had determined ages were assigned to 25-mm length intervals. Age distribution (shown as percent) was identified for each size interval. Thus, the unaged fish were assigned age percentage compositions based on their lengths.

RESULTS AND DISCUSSION

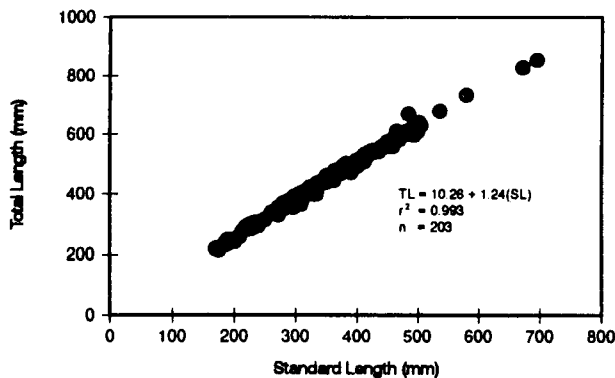
Examination of otoliths.—A total of 537 otolith samples collected from 1990 through 1996 were examined. Two hundred-twenty came from headboat landings, 206 from fishery-independent sampling, and 111 were from red snapper harvested by the commercial hook and line fishery. Of the total, 523 (97.4%) could be aged by counting the number of rings, and 470 (87.5%) were legible enough to record growth measurements. Red snapper were estimated to be ages 1–25. The longevity of 25 yr reported here is greater than that reported by Manooch (1987; Table 7.1) in his review of maximum age and growth parameters for cosmopolitan lutjanids, including 14 species of *Lutjanus*. Results of the current study clearly reveal that red snapper found along the southeastern United States are large, long-lived members of the family Lutjanidae. Red snapper at capture averaged 213 mm TL at age 1, 506 mm at age 5, 763 mm at age 10, 840 mm at age 15, 886 mm at age 20, and 937 mm at age 25 (Table 1).

Validation.—Several observations support the use of otoliths in determining age of red snapper, and validate rings as annual marks. First, the mean lengths of fish increased as the number of rings increased (Tables 1 and 2), second, there was a strong correlation between otolith radii and fish lengths ($r^2 = 0.93$; Fig. 1), and third, marginal increment analyses revealed the formation of rings during March–May (Fig. 2). The latter was confirmed by documenting months when zero marginal increment occurred, January, March, April, and May (Fig. 2). Nel-

a. Fork length - total length



b. Standard length - total length



c. Standard length - fork length

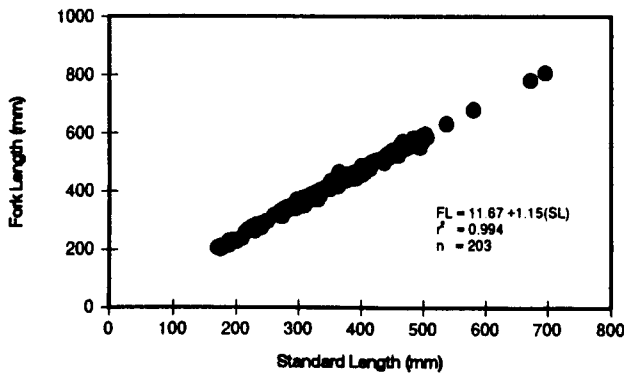


FIG. 6. Length relationships for red snapper off the southeastern U.S.

Table 3. Fish age–fish length key for red snapper off the southeastern U.S.

TL (mm)	Age									
	1	2	3	4	5	6	7	8	9	10
175	1(1.00)									
200	3(1.00)									
225		7(0.88)	1(0.12)							
250		1(1.00)								
275		6(0.60)	4(0.40)							
300		2(0.29)	5(0.71)							
325		1(0.08)	11(0.92)							
350			24(0.73)	9(0.27)						
375			21(0.41)	30(0.59)						
400			14(0.29)	34(0.71)						
425			1(0.03)	21(0.72)	7(0.24)					
450				15(0.48)	16(0.52)					
475				9(0.36)	14(0.56)	2(0.08)				
500				3(0.08)	29(0.76)	6(0.16)				
525					15(0.60)	10(0.40)				
550					12(0.43)	13(0.46)	3(0.11)			
575					2(0.10)	9(0.45)	9(0.45)			
600						21(0.57)	13(0.35)	3(0.08)		
625						5(0.18)	18(0.67)	4(0.15)		
650						8(0.40)	8(0.40)	4(0.20)		
675						1(0.17)	3(0.50)	2(0.33)		
700							8(0.73)	1(0.09)	2(0.18)	
725							1(0.12)	4(0.50)	2(0.25)	1(0.13)
750								3(0.27)	3(0.27)	4(0.37)
775								1(0.10)	2(0.20)	1(0.10)
800										
825										
850										
875										
900										
925										

son and Manooch (1982) had previously found that annuli formed on red snapper otoliths and scales during spring.

Back-calculated growth.—The relationship between fish total length and otolith radius (R_c) is represented by $TL = 1.14 (R_c)^{1.26}$ ($r^2 = 0.93$; $n = 526$; $MSE = 0.006$). Lengths at ages using all data were back-calculated from the otolith proportional equation: $TL = \exp [1.14 + (\ln L_c - 1.14) * (\ln R_A / \ln R_C) + 0.006/2]$. We calculated the mean length of the red snapper at the time of each annulus formation, and the mean annual growth increment at each age (Table 2). Growth appeared most rapid for the first three years of life, then leveled off (Fig. 3; Table 2). Mean back-calculated total lengths ranged from 172 mm at age 1 to 922 mm at age 25.

Growth parameters.—Back-calculated lengths from the last annulus for each age group (Vaughan and Burton, 1994) were used to derive the Bertalanffy growth equation: $L_t = 955 (1 - e^{-0.146(t-0.182)})$. The 95% confidence intervals for L_∞ , K , and t_0 , respectively were: 921–990; 0.134–0.159; and 0.011–0.353. Nelson and Manooch (1982) used scales to age red snapper captured along the southeastern United States, and derived the growth equation: $L_t = 975 (1 - e^{-0.16(t-0.0)})$ (Fig. 4).

Size relationships.—To convert fish lengths into fish weights, we derived the following equation: $W = 1.5 \times 10^{-8} (L)^{2.99}$ ($n = 84$; $r^2 = 0.97$ (Fig. 5), where W = whole weight in kilograms and L = total length in millimeters. Thus, a red

Table 3. Extended.

[illegible]

snapper 200 mm TL is predicted to weigh 0.11 kg; a 600 mm fish, 3.04 kg; and a 900 mm red snapper, 10.22 kg. Nelson and Manooch (1982) derived the equation: $W = 2.04 \times 10^{-5} TL^{2.953}$ for 462 red snapper, where W = weight in grams. Their equation predicted that a 200-mm red snapper weighs 0.13 kg; a 600-mm fish weighs 3.26 kg; and a red snapper 900 mm TL weighs 10.8 kg.

The following linear relationships were calculated to convert fish lengths: TL = $-3.21 + 1.08$ (FL) (n = 240; $r^2 = 0.99$); TL = $10.26 + 1.24$ (SL) (n = 203; $r^2 = 0.99$); and FL = $11.67 + 1.15$ (SL) (n = 203; $r^2 = 0.99$), where FL = fork length in millimeters, and SL = standard length in millimeters (Figure 6).

Fish age-fish length key.—Observed fish lengths and ages at time of capture were used to construct an age-length key (Table 3). The table is readily interpreted. As an example, red snapper that are 175–199 mm total length at capture, indicated by the 175-mm size interval, are all (100%) age 1 fish.

Management.—This study's results were used as the basis for updating an assessment of the red snapper stock along the southeastern United States (Manooch et al. 1997). The current status of the stock was evaluated by utilizing age-specific mortality rates, commercial and recreational landings data, and reproductive biology information, which were used together to yield spawning potential ratio (SPR) and yield per recruit (YPR) estimates. The species appears to be responding well to a 508 mm TL minimum size limit imposed in 1992, and a two fish bag limit implemented in 1992 by the South Atlantic Fishery Management Council.

Acknowledgments. We are grateful for the efforts of NMFS port agents Deborah Codella at Murrells Inlet, SC and Claudia Dennis at New Smyrna Beach, FL for obtaining data and otolith samples from red snapper landed by recreational and commercial fisheries. Jack McGovern, SCDNR, Charleston, SC, provided materials and data obtained from MARMAP fishery-independent sampling. Dean Ahrenholz and Joe Smith, NMFS, Beaufort Laboratory, Beaufort, NC, and Bill Richards and Joe Powers, NMFS, Miami Laboratory, Miami, FL, reviewed various revisions of our manuscript.

REFERENCES CITED

- CARLANDER, K. 1981. Caution on the use of the regression method of back-calculated lengths from scale measurements. *Fisheries*, **6**(1):2-4.
- COWAN, J. H., JR., R. L. SHIPP, H. K. BAILEY, IV, AND D. W. HAYWICK. 1995. Procedure for rapid processing of large otoliths. *Trans. Am. Fish. Soc.* **124**:280-282.
- EVERHART, W. H., A. W. EIPPER, AND W. D. YOUNGS. 1981. *Principles of Fishery Science*, 2nd ed. Cornell Univ. Press, Ithaca, NY, 349 p.
- JOHNSON, A. J., L. A. COLLINS, AND C. P. KEIM. 1994. Age-size structure of gray snapper from the southeastern United States: a comparison of two methods of back-calculating size at age from otolith data. *Proc. Ann. Conf. Southeast. Assoc. Fish Wildl. Agencies*. **49**:592-600.
- MANOOCH, C. S., III. 1984. *Fisherman's guide to the fishes of the southeastern United States*. N.C. Mus. Nat. Hist. Raleigh, NC, 364 p.
- . 1987. Age and growth of snappers and groupers, pp. 329-372. in J. Polovina and S. Ralston (eds.), *Tropical Snappers and Groupers: Biology and Fisheries Management*. Westview Press, Boulder, CO.
- , J. C. POTTS, D. S. VAUGHAN, AND M. L. BURTON. 1997. Population assessment of the red snapper, *Lutjanus campechanus*, from the southeastern United States. Rept. prepared for the South Atlantic Fish. Mgt. Council, Charleston, SC, April 1997, 84 p.
- NELSON, R. S., AND C. S. MANOOCH, III. 1982. Growth and mortality of red snapper, *Lutjanus campechanus*, in the west central Atlantic Ocean and the northern Gulf of Mexico. *Trans. Am. Fish. Soc.* **111**:465-475.
- RICKER, W. E. 1975. Computations and interpretations of biological statistics of fish populations. *Bull. Fish. Res. Bd. Can.* **191**. 382 p.
- SAS INSTITUTE, INC. 1982. *SAS User's Guide: Statistics*. SAS Institute, Cary, NC, 584 p.
- SOUTH ATLANTIC FISHERY MANAGEMENT COUNCIL (SAFMC). 1983. Source document for the snapper-grouper fishery of the south Atlantic region. SAFMC, Charleston, SC 29407.
- VAUGHAN, D. S., AND M. L. BURTON. 1994. Estimation of von Bertalanffy growth parameters in the presence of size-selective mortality: a simulated example with red grouper. *Trans. Am. Fish. Soc.* **123**:1-8.

Received 11 June 1997